

Research Article

The invasive amphipod *Gammarus tigrinus* Sexton, 1939 displaces native gammarid amphipods from sheltered macrophyte habitats of the Gulf of Riga

Greta Reisalu*, Jonne Kotta, Kristjan Herkül and Ilmar Kotta

Estonian Marine Institute, University of Tartu, Mäealuse 14, Tallinn 12618, Estonia

*Corresponding author

E-mail: greta.reisalu@ut.ee

Received: 28 April 2015 / Accepted: 13 October 2015 / Published online: 11 December 2015

Handling editor: Amy Fowler

Abstract

The North-American amphipod *Gammarus tigrinus* Sexton, 1939 is a successful invader in European waters due to its high reproductive potential and tolerance to severe environmental conditions and various pollutants. In this study, we followed the invasion and establishment of this exotic species in a species-poor ecosystem of the northern Baltic Sea. Two years after the establishment of *G. tigrinus*, over half of the sampling sites were occupied exclusively by *G. tigrinus*, whereas *G. tigrinus* coexisted with native gammarids in only one tenth of all sites. There was a clear separation of habitat occupancy between native species and *G. tigrinus* in terms of abiotic environment and macrophytic habitat. *G. tigrinus* preferred shallow sheltered areas dominated by vascular plants, while native species mainly occurred in more exposed, deeper habitats with phaeophytes and rhodophytes. In its suboptimal habitats, *G. tigrinus* exhibited moderate abundances, which allowed for the coexistence of native gammarids and the invasive gammarid. Since its establishment, the abundance of *G. tigrinus* has showed no signs of decline, with abundances exceeding almost fifteen times those of native gammarids at some locations. The results suggest that, irrespective to the competitive superiority of *G. tigrinus* over the native gammarids, the invasive *G. tigrinus* does not monopolize the entire coastal area of the northern Baltic Sea but mostly outcompetes native species in its favoured habitats.

Key words: non-native, nonindigenous, temporal trends, microhabitat, spatial distribution, competition, brackish

Introduction

Human activities seriously modify the geographical distribution of species either by intentional or accidental introductions (Di Castri 1989), which can cause large-scale ecological changes and economic damage worldwide. There are many examples of invasions from the 1980s and 1990s that show how successful exotics may cause previously stable systems to become unbalanced and unpredictable (Carlton 1996; Ruiz et al. 1999) and may severely affect biological diversity in the area (Baker and Stebbins 1965; Levine and D'Antonio 1999).

The Baltic Sea is enclosed by land and is connected to the Atlantic by narrow outlets at its south-western end. Owing to its isolation, relatively short geological age, and dynamic salinity and temperature conditions, only a limited number of species have been able to inhabit this unique brackish water environment.

The resident communities are characterised by a peculiar mixture of generalists, mainly from marine and fresh water origin. Specific brackish water or endemic forms are nearly absent (Hällfors et al. 1981). In the northern Baltic Sea, each ecosystem function is often represented by a single species (Elmgren and Hill 1997). Thus, the loss or addition of a species may correspond to the loss or addition of ecosystem function.

The Baltic Sea has been often regarded as very exposed and sensitive to biological invasions due to its environmental instability, low number of native species, and increasing intensity of freight transportation (Elmgren and Hill 1997; Gollasch and Leppäkoski 1999; Leppäkoski et al. 2002; Paavola et al. 2005). Alternatively, it can be argued that the harsh conditions of the Baltic Sea reduce invasion potential, as only a small number of species are able to survive in such harsh conditions (Bonsdorff 2006). Exotic estuarine species, however, are usually very competitive and

tolerate a wide range of environmental conditions (Packalén et al. 2008; Sareyka et al. 2011). Moreover, many successful global exotics inhabit brackish waters at salinities similar to the Baltic Sea area (Leppäkoski and Olenin 2001). Thus, it is not surprising that, following the recent increase in shipping activity (HELCOM 2010), a large proportion of benthic animals presently living in the Baltic have only recently invaded the area (Kotta 2000; Leppäkoski and Olenin 2001; Laine et al. 2006; Herkül et al. 2009; Kalinkina and Berezina 2010; Kotta and Kuprijanov 2012; Kotta and Ojaveer 2012). A few of these non-native animals add unique ecological functions for the species-poor Baltic Sea ecosystem (Leppäkoski et al. 2002), whereas others share the same food resources with the local species and thus may reduce the diversity and abundances of native species (Kotta et al. 2001; Kotta and Ólafsson 2003).

Gammarid amphipods are among the most important nekto-benthic omnivores in many coastal seas (MacNeil et al. 1997, 1999). The species in this family are abundant in vegetated areas (Kotta et al. 2010); however, in many coastal areas their distribution in the various habitats is not well known, partly due to limited taxonomical resolution applied when sorting field samples. In the northern Baltic Sea, as in many areas, members of the family Gammaridae commonly are identified to the genus level at best (Korpinen and Westerborn 2010).

Five native gammarid species occur in sympatry in the northern Baltic Sea: *Gammarus oceanicus* Segerstråle, 1947; *G. salinus* Spooner, 1947; *G. zaddachi* Sexton, 1912; *G. locusta* (Linnaeus, 1758); and *G. duebeni* Liljeborg, 1852 (Hällfors et al. 1981; Kotta 2000; Packalén et al. 2008; Korpinen and Westerborn 2010). Besides native gammarids, the non-indigenous *Gammarus tigrinus* Sexton, 1939 has inhabited the region since 2003 (Kotta et al. 2006). This species was introduced to Europe from North America and was first recorded in England in 1931 (Sexton and Cooper 1939). *G. tigrinus* expanded into the Baltic Sea in 1975 (Bulnheim 1976) and became widespread during the 1990s and 2000s (Jazdzewski et al. 2002; Szaniawska et al. 2003; Pienimäki et al. 2004; Paavola et al. 2005; Daunys and Zettler 2006; Kotta et al. 2006; Berezina 2007). *G. tigrinus* is thought to have broad ecological tolerances in terms of salinity (Bousfield 1973; Normant et al. 2007), temperature, and pollution (Savage 1996; Sareyka et al. 2011). The species is aggressive (Orav-Kotta et al. 2009) and has higher fecundity and earlier maturation than the native species

(Chambers 1977; Pinkster et al. 1977; Grabowski et al. 2007; Sareyka et al. 2011). Thus, *G. tigrinus* has a potential to become invasive within the Baltic Sea.

Earlier experimental studies have demonstrated that interspecific competition occurs between the native gammarids and *G. tigrinus* in the European fresh and brackish waters (Jazdzewski et al. 2004; Berezina 2007; Packalén et al. 2008; Kotta et al. 2011). In enclosed lagoons and inland waterbodies of the southern Baltic Sea, the native gammarids have either disappeared, or their densities have decreased greatly, concurrent with the spread of *G. tigrinus* (e.g. Pinkster et al. 1992; Jazdzewski et al. 2002; Grabowski et al. 2006). Moreover, in the northern Baltic Sea *G. tigrinus* is able to expand into less nutrient-rich and more wave exposed areas, where the species often forms dense populations (Kotta et al. 2013). To date, we are not aware if this possible range expansion is accompanied with the retreat of native gammarids in such habitats. Therefore, the aims of this paper were to (1) document the establishment success of *G. tigrinus* in various coastal sea habitats of the northern Baltic Sea, (2) quantify the habitat range of *G. tigrinus* and native gammarids, and (3) analyse the overlap between invasive and native gammarid distributions.

Material and methods

This study was conducted in the southern coastal waters of Saaremaa Island, Northern Gulf of Riga, Baltic Sea (Figure 1). The area is characterised by many small bays, peninsulas, and istlets. Sandy sediments dominate in the area, but muddy sand prevails in sheltered bays, and sand mixed with gravel is found in more exposed shallow areas. Scattered boulder fields and stand-alone boulders can be found throughout the area. Salinity is between 4.5 and 6, and the area is influenced by diffuse nutrient loading from the moderately eutrophic Gulf of Riga (Astok et al. 1999). The benthic vegetation is well developed, and extensive proliferation of ephemeral macroalgae and the appearance of drift algal mats have been reported from the area in recent years (Paalme et al. 2004; Lauringson and Kotta 2006).

Benthic macroinvertebrates were sampled quantitatively during two field programs: (1) large spatial-scale sampling covering the whole southern coastal waters of Saaremaa Island in summer 2005; and (2) long-term sampling program in Kõiguste Bay between 2004 and 2013 (Figure 1).

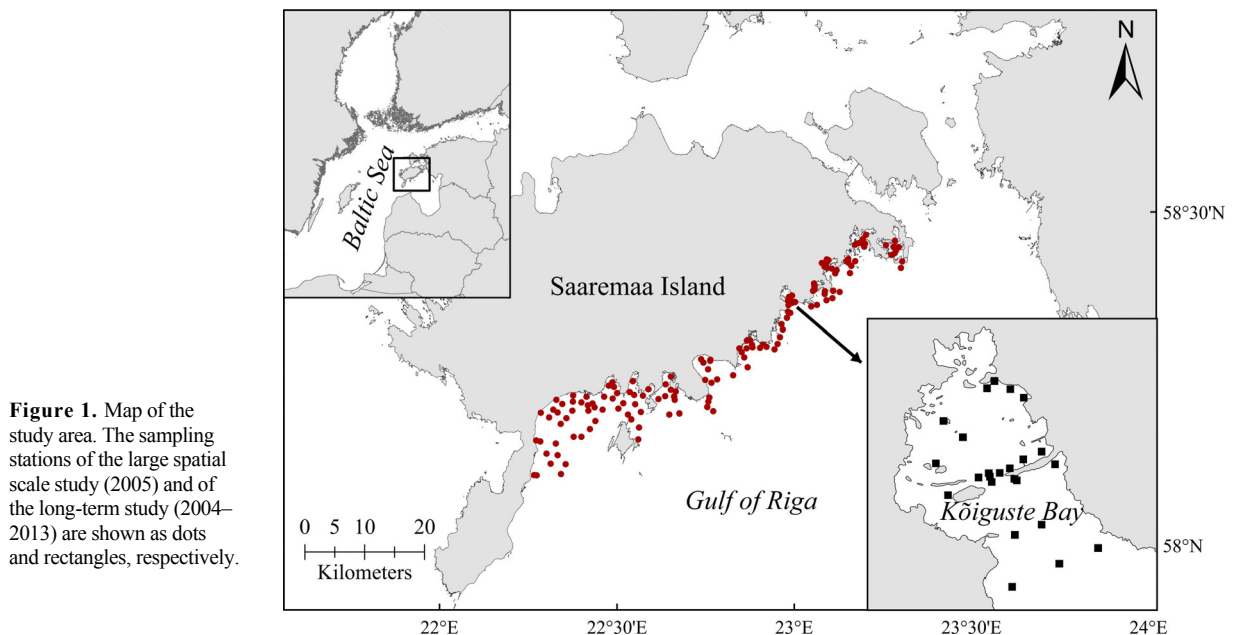


Figure 1. Map of the study area. The sampling stations of the large spatial scale study (2005) and of the long-term study (2004–2013) are shown as dots and rectangles, respectively.

The aim of the large spatial scale sampling was to study the distribution and coexistence of native and invasive gammarids, as well as the habitat occupancy of all gammarid species along a broad environmental gradient (Table 1). Altogether, 150 sites were sampled using an Ekman-type bottom grab (0.02 m²). Three replicate samples were collected from each site. For each site, substrate type (clay, silt, sand, gravel) and depth was recorded. The samples were sieved in the field on 0.25-mm mesh screens, and the residual was stored in a freezer at –18 °C until analysis. In the laboratory, all samples were sorted under a binocular microscope (20–40× magnification). All macrobenthic species were identified to the species level, except for oligochaetes, chironomid larvae, and juveniles of gammarid amphipods (size < 5 mm). Individuals of all taxa were counted and weighed. Prior to weighing, animals and plants were dried at 60 °C for 48 hours and two weeks, respectively. Abundances and biomasses were expressed on a per square metre basis.

To study interannual variability of benthic macroinvertebrate communities, a long term sampling program in Kõiguste Bay was conducted over 10 years. Kõiguste Bay is divided into sheltered northern and moderately exposed southern parts. In the sheltered part of the bay, the average water depth is 0.5–2 m (max 3.5 m), and, in the outer part of the bay, the values are 2–5 m (max 10 m). Salinity varies between 4.5

and 5 but can be slightly lower in the inner parts of the bay due to runoff from a seasonal stream. Wave exposure is about five times lower in sheltered parts of the bay as compared to moderately exposed parts of the bay. In the sheltered areas, benthic vegetation grows to a depth of 2 m whereas in more exposed areas, due to greater water transparency, vegetation can be found at depths of 3–4 m. The study included 24 sampling stations, 12 sites being situated in sheltered areas of the bay and 12 sites in exposed parts of the bay. Sampling was carried out annually in September or October. At this time, the proportion of adults was the highest in gammarid communities, which enabled proper identification of species. The sampling procedure was the same as in the large-scale sampling program.

To analyse the relationships between environmental variables and species abundances/biomasses, canonical correspondence analysis (CCA) in the package “vegan” (Oksanen et al. 2013) of the statistical software R (version 3.0.0) was used. Environmental variables included in the analyses were substrate type, depth, slope of seabed, wave exposure (Nikolopoulos and Isæus 2008), distance to land, distance to 20-m depth isoline, and biomass of macrophytes (brown, red and green algae; phanerogams; and charophytes). Statistical significance of the relationships between environmental variables and gammarid abundances/biomasses in CCA ordination was tested using the permutation

Table 1. Minimum, mean, and maximum values of environmental variables from southern coastal waters of Saaremaa in 2005.

Environmental variable	Minimum	Mean	Maximum
Depth, m	0.3	3.5	10
Soft sediments, %	0	59	100
Distance to land, m	3.3	886.7	5986.9
Distance to 20 m depth isoline, m	7086.8	14032.2	21838.1
Slope of seabed, degrees	0	0.19	2.52
Wave exposure, m ² s ⁻¹	370.5	157490	429171
Biomass of brown algae, g m ⁻²	0	22.60	750.42
Biomass of green algae, g m ⁻²	0	4.24	375.01
Biomass of red algae, g m ⁻²	0	7.79	379.54
Biomass of charophytes, g m ⁻²	0	36.98	3243.26
Biomass of vascular plants, g m ⁻²	0	20.96	701.01

test ($n = 9999$) included in the package “vegan” (Oksanen et al. 2013). In this permutation test, the distribution of the test statistic (R^2 in our case) was obtained by calculating all possible values of the test statistic by randomly rearranging the labels on the observed data points. Given the α -level of 0.05, when an observed R^2 was outside of the 95% of permutationally calculated values, the R^2 value was considered as statistically significant. Statistically nonsignificant environmental variables were eliminated from the final analyses. When analysing distributions of gammarid amphipods, only adult gammarids with body length > 5 mm were included.

Results

Large-scale sampling

Four gammarid amphipod species (*G. salinus*, *G. oceanicus*, *G. zaddachi*, and *G. tigrinus*) were identified during the large-scale sampling campaign. Out of 150 sampling sites, 86 were occupied by gammarids. Of these, 44 sites were occupied exclusively by *G. tigrinus* and it co-occurred with native gammarids in 8 sites (Figure 2). Among native gammarids, *G. salinus*, *G. oceanicus*, and *G. zaddachi* were found either separately or mixed with other native gammarids at 20, 10, and 4 sites, respectively. From locations where only native gammarids were found, the three species co-occurred in 7 sites.

We found a clear separation of habitat occupancy between native and invasive species in terms of abiotic environmental conditions and macrophytes (Figure 3, 4). *G. tigrinus* inhabited shallow, nearshore, sheltered areas characterized by soft

sediments and macrophyte communities dominated by vascular plants (mainly *Myriophyllum spicatum* L.; and *Stuckenia pectinata* (L.) Börner, 1912). Native gammarids inhabited deeper and more wave exposed areas with macrophyte communities dominated by phaeophytes (*Battersia arctica* (Harvey) Draisma, Prud'homme and H. Kawai, 2010; *Fucus vesiculosus* Linnaeus, 1753; *Pylaiella littoralis* (L.) Kjellman, 1872) and rhodophytes (*Furcellaria lumbricalis* (Hudson) J. V. Lamouroux, 1813; *Polysiphonia fucoides* (Hudson) Greville, 1824). *G. tigrinus* was found at a mean depth of 1.9 m but was found at one location at a depth of 5 m. Native gammarid species inhabited a depth range between 0.3 and 10 m, with a mean depth of 4 m.

The abundance and biomass of *G. tigrinus* was significantly higher in the samples where it was the only gammarid species present compared to samples where it co-occurred with native gammarids (ANOVA, $F_{4,190} = 3.917$; $P < 0.05$). In samples without native gammarids, the average (\pm SE) abundance of *G. tigrinus* was 508 ± 110 ind.m⁻² and the average biomass was 0.77 ± 0.19 g m⁻². In samples where both *G. tigrinus* and native gammarids were found, the average abundance and biomass of *G. tigrinus* was much lower: 110 ± 22 ind.m⁻² and 0.14 ± 0.03 g m⁻², respectively. Similarly, the average abundances and biomasses of native gammarids were somewhat higher when *G. tigrinus* was not present (146 ± 29 ind.m⁻² and 0.39 ± 0.06 g m⁻²) compared to samples where native species co-occurred with *G. tigrinus* (136 ± 60 ind.m⁻², 0.27 ± 0.13 g m⁻²); however, the means were not statistically significant ($P > 0.05$). Native gammarids did not co-occur with *G. tigrinus* where the abundance of the alien species exceeded 250 ind.m⁻².

Figure 2. Distribution of gammarid species based on the large spatial scale study in 2005 (n = 150 stations). The diagram shows the proportions of sampling stations occupied by either native (various combinations of *Gammarus salinus*, *G. oceanicus*, and *G. zaddachi*), invasive (*G. tigrinus*), or both groups of amphipods (n = 86 stations).

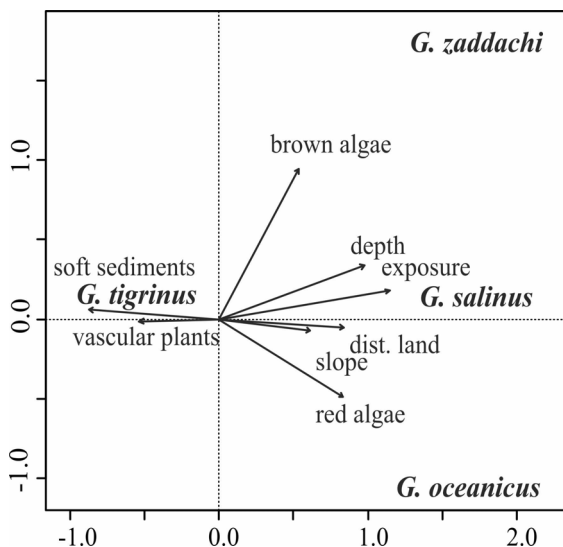
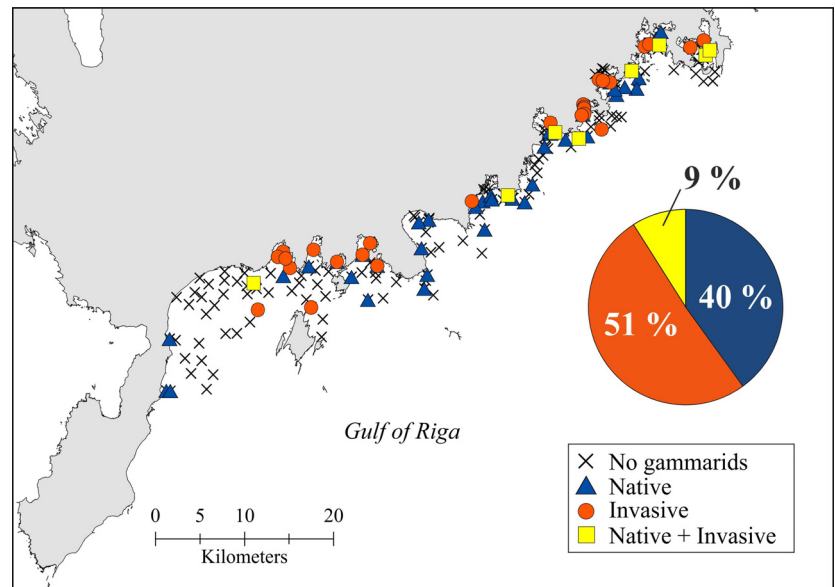


Figure 3. Results of CCA ordination of abundances of gammarid taxa in relation to the environmental variables in the large spatial scale study (2005).

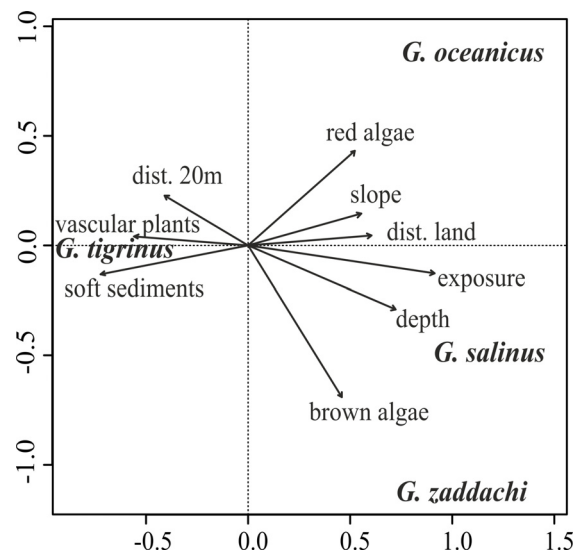


Figure 4. Results of CCA ordination of biomasses of gammarid taxa in relation to the environmental variables in the large spatial scale study (2005).

Long-term sampling

During the long-term sampling campaign, the same gammarid amphipod species were collected as in the large-scale sampling program. The average biomass and abundance of *G. tigrinus* was about fifteen times greater than those of the native species (Figure 5). Over the last ten years, there has not been a significant change in the abundance nor biomass of *G. tigrinus* at the study

sites. The highest average biomass of *G. tigrinus* was recorded as early as 2004. Over the study period, the frequency of occurrence of native gammarids has remained almost the same. In general, *G. tigrinus* had the highest densities in the inner parts of Kõiguste Bay (Figure 6). *G. tigrinus* occurred between 0.5–6.0 m, with a mean water depth of 2 m. The average abundance of *G. tigrinus* was 220 ind.m⁻² but half of the samples

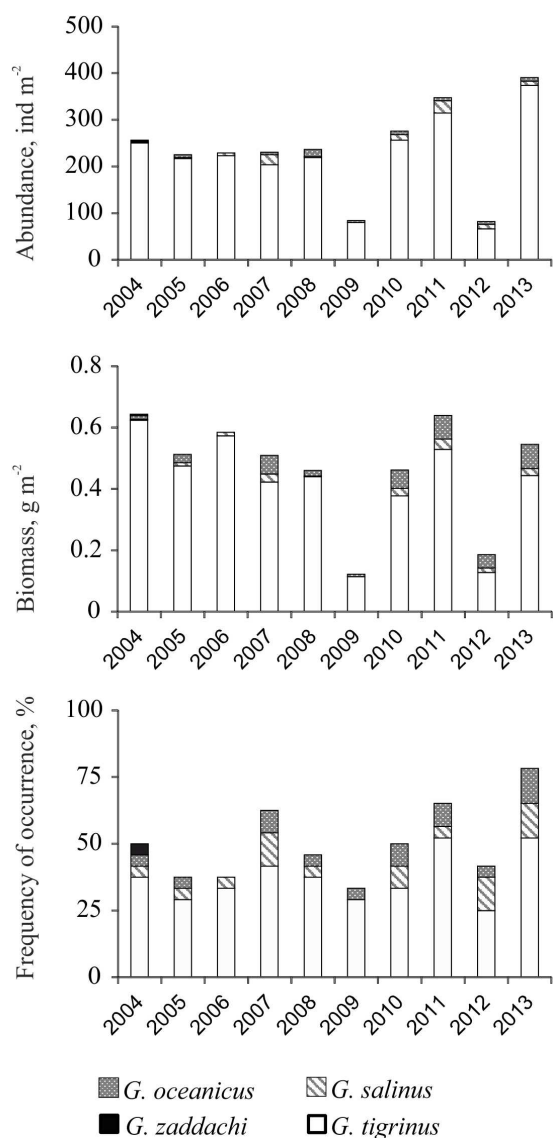


Figure 5. Average abundance, biomass, and frequency of occurrence of different *Gammarus* species in Kõiguste Bay in 2004–2013. *G. zaddachi* was found only in 2004 in a single sampling site.

exceeded 350 ind.m⁻² and the largest single estimate was 4,700 ind.m⁻². As would be expected, in such areas *G. tigrinus* comprised 100% of the gammarids sampled.

The native gammarids had high densities only in the more exposed bay areas. Among native gammarids, *G. salinus* was dominant with a maximum abundance of 611 ind.m⁻². Over the study period, we found only a single individual of *G. zaddachi*, and the specimen was collected in 2004 from the outer bay area at 5 m depth.

Long term sampling showed similar habitat occupancy for *G. tigrinus* related to abiotic environmental conditions and macrophytes as in the large-scale sampling program. We did not find any gammarid species from four sampling sites in the outer bay area. These sites were characterised by high exposure to the waves and low macrophyte biomass.

Discussion

In the northern Gulf on Riga, the North-American amphipod *G. tigrinus* has become a successful and widespread species since its introduction in 2003–2004 (Kotta 2000; Orav-Kotta 2004; Herkül et al. 2006; Lauringson and Kotta 2006). At the same time, *G. tigrinus* was also found along the Finnish coast of the Gulf of Finland (Pienimäki et al. 2004). *G. tigrinus* is now a dominant gammarid with a high density and biomass in numerous habitats throughout the northern Baltic Sea (e.g. Herkül and Kotta 2007; Kotta et al. 2013).

Our spatial survey data showed a clear differentiation in habitat occupancy between native and the invasive species. While *G. tigrinus* is thought to have a broad ecological niche (Steele and Steele 1972; Bousfield 1973), our surveys showed that *G. tigrinus* was primarily found in sheltered shallow water areas with soft sediments. These areas are dominated by vascular plants due to low salinity and low occurrence of hard substrate. *G. tigrinus* was occasionally found at macroalgae dominated habitats but at much lower densities. Thus, it leaves the macroalgae as refugium for native species. This is in agreement with earlier studies from the Baltic Sea area (Jazdzewski et al. 2002; Jazdzewski et al. 2004; Szaniawska et al. 2003; Daunys and Zettler 2006; Herkül and Kotta 2007; Packalén et al. 2008; Kotta et al. 2013) and may be explained by the higher tolerance of *G. tigrinus* to fluctuating environmental conditions (e.g. salinity and hypoxia) in such habitats (Bousfield 1973; Winn and Knott 1992; Platvoet and Pinkster 1995; Gerhardt and Quindt 2000). Within these sheltered habitats, *G. tigrinus* has higher abundances and biomasses than native gammarid species in any of the studied habitats. The habitats that were densely populated by *G. tigrinus* are not of the highest suitability for the native gammarids that are of marine origin and thus adapted to hard substrate vegetation zone of more marine conditions (higher salinity, elevated wave exposure) (Yarvekyul 1979). Based

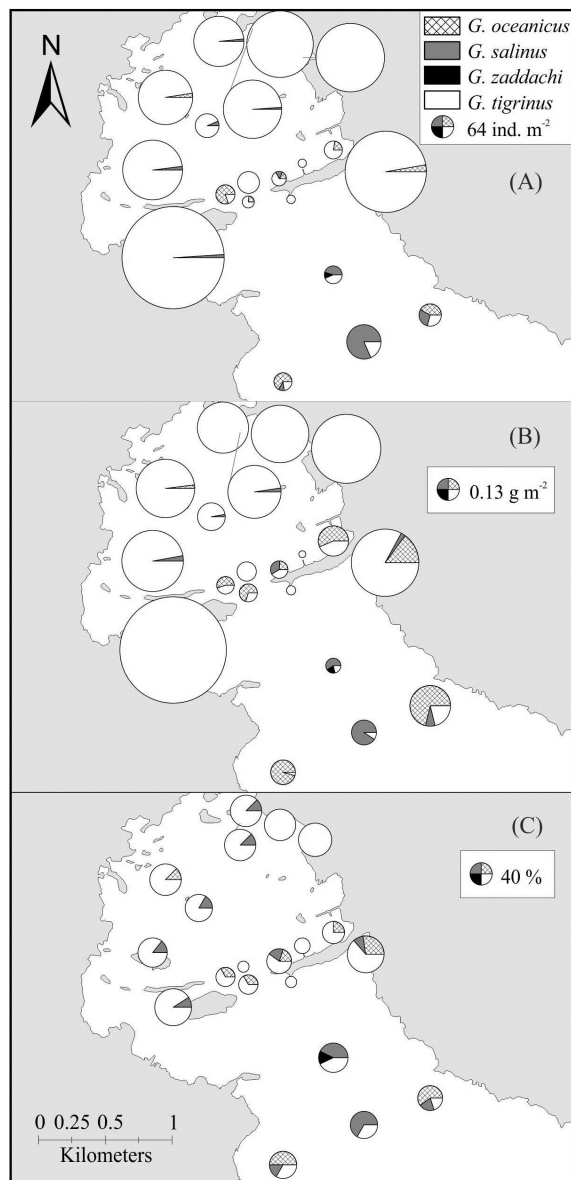


Figure 6. Average (A) abundance, (B) biomass, (C) frequency of occurrence of gammarids in the inner and outer part of the Kõiguste Bay in 2004–2013. In the legend, the number next to the pie chart symbol represents the value of abundance, biomass, and frequency of occurrence for a pie chart symbol of that size on the map.

on the historical records (e.g. Kotta et al. 1998), the native gammarids were present in the habitats that are now colonized by *G. tigrinus*, but with lower abundances than in more marine habitats. Thus, *G. tigrinus* has primarily colonized areas where the abundance of native gammarids was lower. In these sub-optimal habitats the density and fitness of native species are already lower and therefore they are possibly more

susceptible to the competitive and predation pressure exerted by *G. tigrinus*.

In terms of geographic space, the shallow sheltered bays favourable to *G. tigrinus* have smaller area compared to the more exposed coastal areas in the study region. Based on that and the results of the CCA ordination showing strong habitat segregation between *G. tigrinus* and native species, we can assume that *G. tigrinus* will not totally monopolize the coastal environment.

There are numerous studies reporting the decline of abundance of *G. zaddachi* after an invasion by *G. tigrinus* (Pinkster et al. 1977; Jazdzewski et al. 2004; Grabowski et al. 2006). Both *G. zaddachi* and *G. tigrinus* prefer shallow waters and occupy the same depths and even the same micro-habitats (Bousfield 1973; Grigorovich et al. 2005; Packalén et al. 2008; Korpinen and Westerborn 2010). An alternative reason for disappearance of *G. zaddachi* could be that the species has smaller broods (Sareyka et al. 2011) and longer maturation times than *G. tigrinus* (Pinkster et al. 1977). Similarly, the combined effect of predation on native juvenile amphipods and large brood production of *G. tigrinus* has been experimentally demonstrated to favour *G. tigrinus* over *G. duebeni* (Jänes et al. 2015). Moreover, *G. tigrinus* has a longer and earlier breeding season, which enables individuals to reach full body size by the time native gammarids start to breed (Wawrzyniak-Wydrowska and Gruszka 2005). Thus, *G. tigrinus* can exert predation pressure on the juveniles of native gammarids immediately after their appearance.

Availability of refuge can be one reason why *G. tigrinus* had significantly lower abundance in more exposed habitats. The predation by three-spined stickleback *Gasterosteus aculeatus* Linnaeus, 1758 induces a significant mortality on *G. tigrinus*, and, in general, the abundance of sticklebacks is higher in moderately exposed than in sheltered habitats (Kotta et al. 2010). The study area is relatively eutrophic, characterised with lush vegetation and dense populations of associated benthic invertebrates. As such, the plethora of diverse dietary options suggests that competition between the native and invasive gammarids for food is not likely. During winter, however, the potential for competition may be intensified as the bulk of benthic biomass is comprised of perennial vegetation and a few invertebrate prey.

Based on our long-term data, the abundance of *G. tigrinus* in Kõiguste Bay has been relatively stable over the last ten years, which indicates that *G. tigrinus* has formed a permanent population in northern Gulf of Riga. In the 1970s, however,

local gammarids, including *G. locusta*, *G. zaddachi*, *G. salinus*, and *G. oceanicus* prevailed in the areas that are now dominated by *G. tigrinus* (Kotta et al. 1998). Thus, concurrent with the establishment of the invasive species, *G. tigrinus* has likely forced the native gammarids out of some of their habitat. In its native range, the distribution area of *G. tigrinus* partly overlaps with some gammarid species that are also common in the Baltic Sea area, but due to the differences in salinity tolerance these species rarely co-exist (Steele and Steele 1972). In the Baltic Sea, however, many euryhaline species widen their ecological range due to low and stable salinities compared to typical estuarine habitats (Dahl 1973; Fenchel and Kolding 1979). Therefore the distribution of *G. tigrinus* may partly overlap with those of *G. oceanicus*, *G. salinus*, and *G. zaddachi*.

To conclude, there are numerous fine-scale experimental studies showing negative effects of *G. tigrinus* on native gammarids in the Baltic Sea. Our field observations together with historical reports on the distribution of native gammarids demonstrated that, at the basin scale, *G. tigrinus* is replacing native gammarids in some specific habitats. Our study also suggested that, irrespective to the competitive superiority of *G. tigrinus* over the native gammarids, the invasive *G. tigrinus* does not monopolize all of the coastal areas of the northern Baltic Sea but mostly intensifies the role of amphipods in sheltered macrophyte habitats. Native species can still be successful in habitats sub-optimal for *G. tigrinus*.

Acknowledgements

We sincerely thank two anonymous reviewers. Funding for this research was provided by Institutional research funding IUT02-20 of the Estonian Research Council and the BONUS project BIO-C3, the joint Baltic Sea research and development programme (Art 185), funded jointly from the European Union's Seventh Programme for research, technological development and demonstration and from the Estonian Research Council.

References

- Astok V, Otsmann M, Suursaar Ü (1999) Water exchange as the main physical process in semi-enclosed marine systems: the Gulf of Riga case. *Hydrobiologia* 393: 11–18, <http://dx.doi.org/10.1023/A:1003517110726>
- Baker H, Stebbins G (eds) (1965) The Genetics of Colonizing Species. Proceedings of the First International Union of Biological Sciences Symposia on General Biology, Academic Press, New York, 588 pp
- Berezina NA (2007) Expansion of the North American amphipod *Gammarus tigrinus* Sexton, 1939 to the Neva Estuary (easternmost Baltic Sea). *Oceanologia* 49: 129–135
- Bonsdorff E (2006) Zoobenthic diversity-gradients in the Baltic Sea: Continuous post-glacial succession in a stressed ecosystem. *Journal of Experimental Marine Biology and Ecology* 330(1): 383–391, <http://dx.doi.org/10.1016/j.jembe.2005.12.041>
- Bousfield EL (1973) Shallow-water Gammaridean Amphipoda of New England. Cornell University Press, Ithaca, 312 pp
- Bulnheim HP (1976) *Gammarus tigrinus*, ein neues Faunenelement der Ostseeförde Schlei. *Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein* 46: 79–84
- Carlton JT (1996) Pattern, process, and prediction in marine invasion ecology. *Biological Conservation* 78: 97–106, [http://dx.doi.org/10.1016/0006-3207\(96\)00020-1](http://dx.doi.org/10.1016/0006-3207(96)00020-1)
- Chambers MR (1977) The population ecology of *Gammarus tigrinus* (Sexton) in the reed beds of the Tjeukemeer. *Hydrobiologia* 53: 155–164, <http://dx.doi.org/10.1007/BF00029294>
- Dahl E (1973) Ecological range of Baltic and North Sea species. *Oikos* 15: 85–90
- Daunys D, Zettler ML (2006) Invasion of the North American Amphipod (*Gammarus tigrinus* Sexton, 1939) into the Cronian Lagoon, South-Eastern Baltic Sea. *Acta Zoologica Lituanica* 16: 20–26, <http://dx.doi.org/10.1080/13921657.2006.10512705>
- Di Castri F (1989) History of biological invasions with special emphasis on the Old World. In: Drake JA, Mooney HA, di Castri F, Groves RH, Krüger FJ, Rejmanek M, Williamson M (eds), Biological invasions: a global perspective, Scope 37. John Wiley and Sons, Chichester, New York, Brisbane, Toronto, Singapore, pp 1–30
- Elmgren R, Hill C (1997) Ecosystem function at low biodiversity – the Baltic example. In: Ormond RFG, Gage JD, Angel MV (eds), Marine Biodiversity: Patterns and Processes. Cambridge University Press, Cambridge, UK, 460 pp, <http://dx.doi.org/10.1017/CBO9780511752360.015>
- Fenchel TM, Kolding S (1979) Habitat selection and distribution patterns of five species of the amphipod genus *Gammarus*. *Oikos* 33: 316–322, <http://dx.doi.org/10.2307/3544008>
- Gerhardt A, Quindt K (2000) Waste water toxicity and bio-monitoring with *Gammarus pulex* (L.) and *Gammarus tigrinus* (Sexton) (Crustacea: Amphipoda). *Wasser und Boden* 52(10): 19–26
- Gollasch S, Leppäkoski E (1999) Initial risk assessment of alien species in Nordic coastal waters. Nord 8, Copenhagen, Denmark, 244 pp
- Grabowski M, Jazdzewski K, Konopacka A (2007) Alien Crustacea in Polish waters – Amphipoda. *Aquatic Invasions* 2: 25–38, <http://dx.doi.org/10.3391/ai.2007.2.1.3>
- Grabowski M, Konopacka A, Jazdzewski K, Janowska E (2006) Invasions of alien gammarid species and retreat of natives in the Vistula Lagoon (Baltic Sea, Poland). *Helgolander Marine Research* 60: 90–97, <http://dx.doi.org/10.1007/s10152-006-0025-8>
- Grigorovich IA, Kang M, Ciborowski JJH (2005) Colonization of the Laurentian Great Lakes by the Amphipod *Gammarus tigrinus*, a Native of the North American Atlantic Coast. *Journal of Great Lakes Research* 31: 333–342, [http://dx.doi.org/10.1016/S0380-1330\(05\)70264-1](http://dx.doi.org/10.1016/S0380-1330(05)70264-1)
- Hällfors G, Niemi Å, Ackefors H, Lassig J, Leppäkoski E (1981) Biological oceanography. In Voipio A (ed), The Baltic Sea. Elsevier Oceanography Series, Amsterdam, 30, pp 219–274, [http://dx.doi.org/10.1016/S0422-9894\(08\)70142-9](http://dx.doi.org/10.1016/S0422-9894(08)70142-9)
- HELCOM (2010) Maritime Activities in the Baltic Sea – An integrated thematic assessment on maritime activities and response to pollution at sea in the Baltic Sea Region. Baltic Sea Environmental Proceedings No. 123
- Herkül K, Kotta J, Kotta I, Orav-Kotta H (2006) Effects of physical disturbance, isolation and key macrozoobenthic species on community development, recolonisation and sedimentation processes. *Oceanologia* 48: 267–282
- Herkül K, Kotta J (2007) New records of the amphipods *Chelicorophium curvispinum*, *Gammarus tigrinus*, *G. duebeni*, and *G. lacustris* in the Estonian coastal sea. *Proceedings of the Estonian Academy of Sciences: Biology, Ecology* 56: 290–296

- Herkül K, Kotta J, Püss T, Kotta I (2009) Crustacean invasions in the Estonian coastal sea. *Estonian Journal of Ecology* 58: 313–323, <http://dx.doi.org/10.3176/eco.2009.4.06>
- Jänes H, Kotta J, Herkül K (2015) High fecundity and predation pressure of the invasive *Gammarus tigrinus* cause decline of indigenous gammarids. *Estuarine, Coastal and Shelf Science*, 165: 185–189, <http://dx.doi.org/10.1016/j.ecss.2015.05.014>
- Jazdzewski K, Konopacka A, Grabowski M (2002) Four Ponto-Caspian and one American gammarid species (Crustacea, Amphipoda) recently invading Polish waters. *Contributions to Zoology* 71: 115–122
- Jazdzewski K, Konopacka A, Grabowski M (2004) Recent drastic changes in the gammarid fauna (Crustacea, Amphipoda) of the Vistula River deltaic system in Poland caused by alien invaders. *Diversity and Distributions* 10: 81–87, <http://dx.doi.org/10.1111/j.1366-9516.2004.00062.x>
- Kalinkina NM, Berezina NA (2010) First record of *Pontogammarus robustoides* Sars, 1894 (Crustacea: Amphipoda) in the Gulf of Riga (Baltic Sea). *Aquatic Invasions* 5: 5–7, <http://dx.doi.org/10.3391/ai.2010.5.S1.002>
- Korpinen S, Westerborn M (2010) Microhabitat segregation of the amphipod genus *Gammarus* (Crustacea: Amphipoda) in the Northern Baltic Sea. *Marine Biology* 157: 361–370, <http://dx.doi.org/10.1007/s00227-009-1323-x>
- Kotta J (2000) Impact of eutrophication and biological invasions on the structure and functions of benthic macrofauna. PhD Thesis, University of Tartu, Tartu, Estonia, 160 pp
- Kotta J, Herkül K, Kotta I, Orav-Kotta H (2006) Invasion history and distribution of the key benthic alien invertebrate species in the Estonian coastal sea. In: Ojaveer H, Kotta J (eds), Alien invasive species in the north-eastern Baltic Sea: population dynamics and ecological impacts. Estonian Marine Institute Report Series No. 14, pp 13–19
- Kotta J, Orav-Kotta H, Herkül K (2010) Separate and combined effects of habitat-specific fish predation on the survival of invasive and native gammarids. *Journal of Sea Research* 64: 369–372, <http://dx.doi.org/10.1016/j.seares.2010.05.006>
- Kotta J, Kotta I, Martin G, Kuk H (1998) A survey of data published on the littoral zoobenthos of the Gulf of Riga. *Proceedings of the Estonian Academy of Sciences: Biology, Ecology* 47(2): 83–97
- Kotta J, Kuprijanov I (2012) The first finding of the palaemonid shrimp *Palaemon elegans* Rathke in the Estonian coastal sea. *Estonian Journal of Ecology* 61: 148–153, <http://dx.doi.org/10.3176/eco.2012.2.06>
- Kotta J, Ojaveer H (2012) Rapid establishment of the alien crab *Rhithropanopeus harrisi* (Gould) in the Gulf of Riga. *Estonian Journal of Ecology* 61: 293–298, <http://dx.doi.org/10.3176/eco.2012.4.04>
- Kotta J, Ólafsson E (2003) Competition for food between the introduced exotic polychaete *Marenzelleria viridis* and the resident native amphipod *Monoporeia affinis* in the Baltic Sea. *Journal of Sea Research* 342: 27–35, [http://dx.doi.org/10.1016/S1385-1101\(03\)00041-8](http://dx.doi.org/10.1016/S1385-1101(03)00041-8)
- Kotta J, Orav-Kotta H, Herkül K, Kotta I (2011) Habitat choice of the invasive *Gammarus tigrinus* and the native *Gammarus salinus* indicates weak interspecific competition. *Boreal Environment Research* 16: 64–72
- Kotta J, Orav H, Sandberg-Kilpi E (2001) Ecological consequence of the introduction of the polychaete *Marenzelleria viridis* into a shallow water biotope of the northern Baltic Sea. *Journal of Sea Research* 46: 273–280
- Kotta J, Pärnoja M, Katajisto T, Lehtiniemi M, Malavin SA, Reisalu G, Panov VE (2013) Is a rapid expansion of the invasive amphipod *Gammarus tigrinus* Sexton, 1939 associated with its niche selection: a case study in the Gulf of Finland, the Baltic Sea. *Aquatic Invasions* 8: 319–332, <http://dx.doi.org/10.3391/ai.2013.8.3.08>
- Laine AO, Mattila J, Lehtikainen A (2006) First record of the brackish water dreissenid bivalve *Mytilopsis leucophaea* in the northern Baltic Sea. *Aquatic Invasions* 1: 38–41, <http://dx.doi.org/10.3391/ai.2006.1.1.9>
- Lauringson V, Kotta J (2006) Influence of the thin drift algal mats on the distribution of macrozoobenthos in Kõiguste Bay, NE Baltic Sea. *Hydrobiologia* 554: 97–105, <http://dx.doi.org/10.1007/s10750-005-1009-4>
- Leppäkoski E, Olenin S (2001) The meltdown of biogeographical peculiarities of the Baltic Sea: the interaction of natural and man-made processes. *Ambio: A Journal of the Human Environment* 30: 202–209, <http://dx.doi.org/10.1579/0044-7447-30.4.202>
- Leppäkoski E, Olenin S, Gollasch S (2002) The Baltic Sea – a field laboratory for invasion biology. In: Leppäkoski E, Olenin S, Gollasch S (eds), Invasive Aquatic Species of Europe: Distribution, Impacts and Management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 253–259, http://dx.doi.org/10.1007/978-94-015-9956-6_27
- Levine JM, D’Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15–26, <http://dx.doi.org/10.2307/3546992>
- MacNeil C, Dick JTA, Elwood RW (1997) The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda) problems and perspectives concerning the functional feeding group concept. *Biological Reviews* 72: 349–364, <http://dx.doi.org/10.1017/S0006323196005038>
- MacNeil C, Dick JTA, Elwood RW (1999) The dynamics of predation on *Gammarus* spp. (Crustacea: Amphipoda). *Biological Reviews* 74: 375–395, <http://dx.doi.org/10.1017/S0006323199005368>
- Nikolopoulos A, Isæus M (2008) Wave exposure calculations for the Estonian coast. AquaBiota Water Research, 26 pp
- Normant M, Feike M, Szaniawska A, Graf G (2007) Adaptation of *Gammarus tigrinus* Sexton, 1939 to new environments - Some metabolic investigations. *Thermochimica acta* 458: 107–111, <http://dx.doi.org/10.1016/j.tca.2007.01.030>
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013) vegan: Community Ecology Package. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan> (Accessed 2 Feb. 2015)
- Orav-Kotta H (2004) Habitat choice and feeding activity of benthic suspension feeders and mesograzers in the northern Baltic Sea. PhD Thesis, University of Tartu, Tartu, Estonia, 117 pp
- Orav-Kotta H, Kotta J, Herkül K, Kotta I, Paalme T (2009) Seasonal variability in the grazing potential of the invasive amphipod *Gammarus tigrinus* and the native amphipod *Gammarus salinus* (Amphipoda: Crustacea) in the northern Baltic Sea. *Biological Invasions* 11: 597–608, <http://dx.doi.org/10.1007/s10530-008-9274-6>
- Paalme T, Martin G, Kotta J, Kuk H, Kaljurand K (2004) Distribution and dynamics of drifting macroalgal mats in the Estonian coastal waters during 1995–2003. *Proceedings of the Estonian Academy of Sciences: Biology, Ecology* 53: 260–268
- Paavola M, Olenin S, Leppäkoski E (2005) Are invasive species most successful in habitats of low native species richness across European brackish water seas? *Estuarine, Coastal and Shelf Science* 64: 738–750, <http://dx.doi.org/10.1016/j.ecss.2005.03.021>
- Packalén A, Korpinen S, Lehtonen S (2008) The invasive amphipod species *Gammarus tigrinus* (Sexton 1939) can rapidly change littoral communities in the Gulf of Finland (Baltic Sea). *Aquatic Invasions* 3: 405–412, <http://dx.doi.org/10.3391/ai.2008.3.4.5>
- Pienimäki M, Helavuori M, Leppäkoski E (2004) First findings of the North American amphipod *Gammarus tigrinus* Sexton, 1939 along the Finnish coast. *Memoranda Societatis pro fauna et flora Fennica* 80: 17–19
- Pinkster S, Scheepmaker M, Platvoet D, Broodbakker N (1992) Drastic changes in the amphipod fauna (Crustacea) of Dutch inland water during the last 25 years. *Bijdragen tot de Dierkunde* 61(4): 193–204

- Pinkster S, Smit H, Jong NB-d (1977) The introduction of the alien amphipod *Gammarus tigrinus* Sexton, 1939, in the Netherlands and its competition with indigenous species. *Crustaceana* Supplement 4: 91–105
- Platvoet D, Pinkster S (1995) Changes in the amphipod fauna (Crustacea) of the Rhine, Meuse and Scheldt Estuary due to the 'Delta Plan' coastal engineering works. *Netherland Journal of Aquatic Ecology* 29: 5–30, <http://dx.doi.org/10.1007/BF02061786>
- Ruiz GM, Fofonoff P, Hines AH (1999) Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnology and Oceanography* 44: 950–972, http://dx.doi.org/10.4319/lo.1999.44.3_part_2.0950
- Sareyka J, Kraufvelin P, Lenz M, Lindström M, Tollrian R, Wahl M (2011) Differences in stress tolerance and brood size between a non-indigenous and an indigenous gammarid in the northern Baltic Sea. *Marine Biology* 158: 2001–2008, <http://dx.doi.org/10.1007/s00227-011-1708-5>
- Savage AA (1996) Density dependent and density independent relationships during a twenty-seven year study of the population dynamics of the benthic macroinvertebrate community of a chemically unstable lake. *Hydrobiologia* 335: 115–131, <http://dx.doi.org/10.1007/BF00015273>
- Sexton EW, Cooper LHN (1939) On a new species of *Gammarus* (*G. tigrinus*) from Droitwich district. *Journal of the Marine Biological Association of the United Kingdom* 23: 543–551, <http://dx.doi.org/10.1017/S0025315400014065>
- Steele VJ, Steele DH (1972) The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. V. *Gammarus oceanicus* Segerstråle. *Canadian Journal of Zoology* 50: 801–813, <http://dx.doi.org/10.1139/z72-109>
- Szaniawska A, Łapucki T, Normant M (2003) The invasive amphipod *Gammarus tigrinus* Sexton, 1939, in Puck Bay. *Oceanologia* 45(3): 507–510
- Wawrzyniak-Wydrowska B, Gruszka P (2005) Population dynamics of alien gammarid species in the River Odra estuary. *Hydrobiologia* 539: 13–25, <http://dx.doi.org/10.1007/s10750-004-3081-6>
- Winn RN, Knott DM (1992) An evaluation of the survival of experimental populations exposed to hypoxia in the Savannah River estuary. *Marine Ecology-Progress Series* 88: 161–179, <http://dx.doi.org/10.3354/meps088161>
- Yarvekyul'g A (1979) Bottom Fauna in the Eastern Part of the Baltic Sea. Valgus, Tallinn, 382 pp (in Russian)